An Archaic Ungulate of middle Paleocene age from Southeast Montana

Research Thesis

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Abstract

A sample of five associated mammalian teeth collected from the Williston Basin in the Fort Union Formation of southeast Montana demonstrate the occurrence of an archaic ungulate at the School Well Locality, a site of known early middle Paleocene age. Study of interproximal wear facets on the teeth demonstrate that the teeth were adjacent to one another in life and belonged to the same side of the lower dentition of a single individual. Relative extent of wear on the specimens suggests that the animal was a young adult with a tooth eruption sequence typical for a placental mammal. Using character states scored on the specimens and a previously published character-by-taxon data matrix (Zack et al., 2005, and Williamson and Weil, 2011) a provisional assessment of the phylogenetic affinities of the School Well archaic ungulate was made. The matrix was analyzed using TNT (Tree analysis using New Technology), a phylogenetic data analysis program. The analysis produced a consensus tree of the 11 shortest trees, placing the unknown sample within the family-level clade Hyopsodontidae, and further within a subclade containing members of the subfamily Mioclaeninae. Further assessment of the identity and status of the School Well archaic ungulate as a possible new species will focus on comparisons within this subgroup.

Contents

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1. Introduction

With over 5,000 living species on earth, mammals have proven to be some of the most resilient and well adapted organisms ever to exist. Following the extinction of the non-avian dinosaurs at the end of the Cretaceous there was a massive mammalian radiation event that drastically increased the number of unique mammalian species and by the end of the Paleocene there were 85 new families distributed in 20 orders (Rose, 2006). This radiation event began during the Paleocene and continued well into the Eocene, where many of the groups basal to extant mammals find their origins.

Extant mammals can be separated into three clades, the Eutherians (placental mammals) and Metatherians (marsupials) and Monotremata (monotremes). Within the Eutherians lies an extinct order named Condylathra, often referred to as the "Archaic Ungulates", on which this study heavily focuses. Condylarths represent a grade of ungulate evolution that is more advanced than the basal ungulate Zhelestidae but less so than of extant ungulate groups (Rose, 2006).

The North American Land Mammal Ages (NALMAs) divide geologic time into intervals based on successive first appearance events of North American mammalian fauna. The samples discussed throughout this study were collected from a locality thought to be Torrejonian (NALMA,To1-2) in

age. The Torrejonian spans roughly 61-64 million years, beginning with the first appearance of the Condylath *Periptychus carinidens* and ending with the first appearance of the primate *Plesiadapis* (Archibald et al., 1987).

A set of five associated mammalian teeth was previously collected from the School Well locality in the Fort Union formation in southeast Montana by Dr. John P. Hunter in 1994. Preliminary analysis suggested that the individual was a condylarth belonging to the genus *Promioclaenus*. Through the investigation of these samples the objective of this study is to determine whether the specimens belong to a previously described taxon of archaic ungulate or is a species new to science.

The information gathered through the investigation of the School Well samples will aid in increasing the resolution of the biochronological data of nonmarine sediments of the Fort Union Formation. The School Well fauna includes only four species in addition to the sample being discussed in this study including *Paromomys maturus*, which is almost exclusively correlated with the Torrejonian and early Tiffanian. The age of the School Well locality cannot be confidently determined based on this information. However, through the identification of the sample in question, the biochronological age can be more confidently constrained and could aid in describing the timing of various transgressions and regressions of the last vestiges of the Western Interior Seaway (Hartman et al., 1998; Hunter et al., 2003).

i. Geological and Stratigraphic setting

The samples analyzed in this study were collected from the School Well Locality (L6427a, b), which lies on private property northwest of Glendive Montana in sec.17, T. 17N., R. 55 E., Stipek Quadrangle (1967), Dawson County. (Figure 1) The locality was discovered in 1993 and was originally chosen because of the completeness of the stratigraphy representing the K/T transition. With palynomorphs from two separate locations and the identification of a fern spike, the age of the localities can be precisely placed at the K/T boundary (Hunter et al, 1997).

The School Well locality lies in the upper Ludlow Member of the Fort Union Formation (Figure 2). "Lignite near the K/T boundary is referred to as "Contact Coal" in reference to its placement at the contact between the Hell Creek and Fort Union Formations at the base of the Ludlow Member" (Hunter, et al. 1997). The exact distance that the School Well locality lies above the "Contact Coal" is uncertain but estimated to be roughly 60 meters representing an estimated 1.5 million years. The locality can be further constrained by its positioning at roughly six meters above the Poverty Flats Lignite bed (Figure 2) and lies at the base of a series of fossiliferous, fluviodeltaic, sedimentary stacked channel sandstones (Hunter et al, 1997). The School Well locality was originally identified as early Torrejonian (NALMA,To1-To2) based on the School Well Mammalian Local Fauna, which

includes the presence of *Paramomys*, *Litaletes mantiensis* and *Ptilodus montanus*.

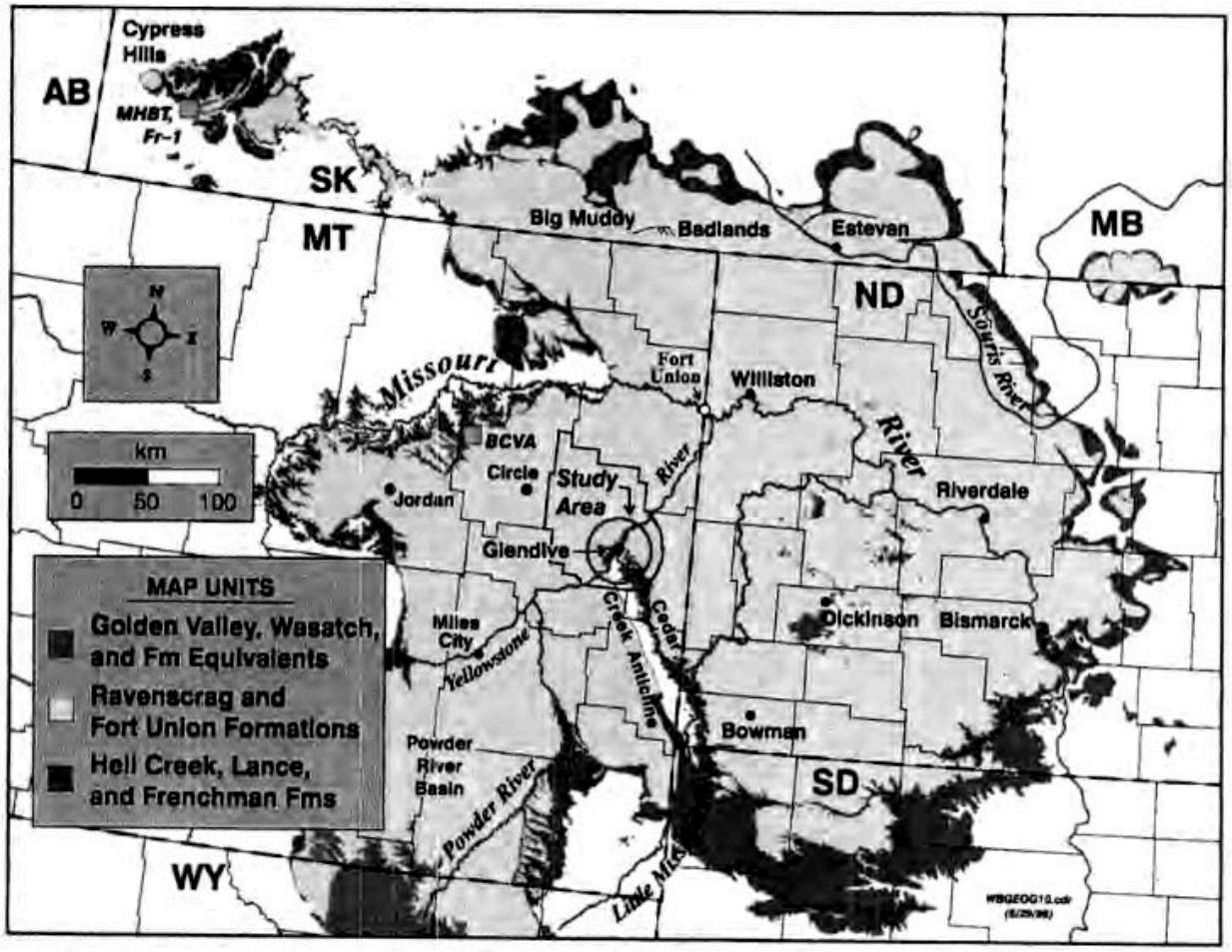


Figure 1*. A map of the highlighted study area near Glendive. The bedrock geology displayed was derived from Clayton(1980), with unpublished data provided by S.M. Vuke of the Montana Bureau of Mines and Geology and Foster Sawer of the South Dakota Geological Survey(see Hartman and Kihm,1995) Map adapted from Hunter et al., 1997.*

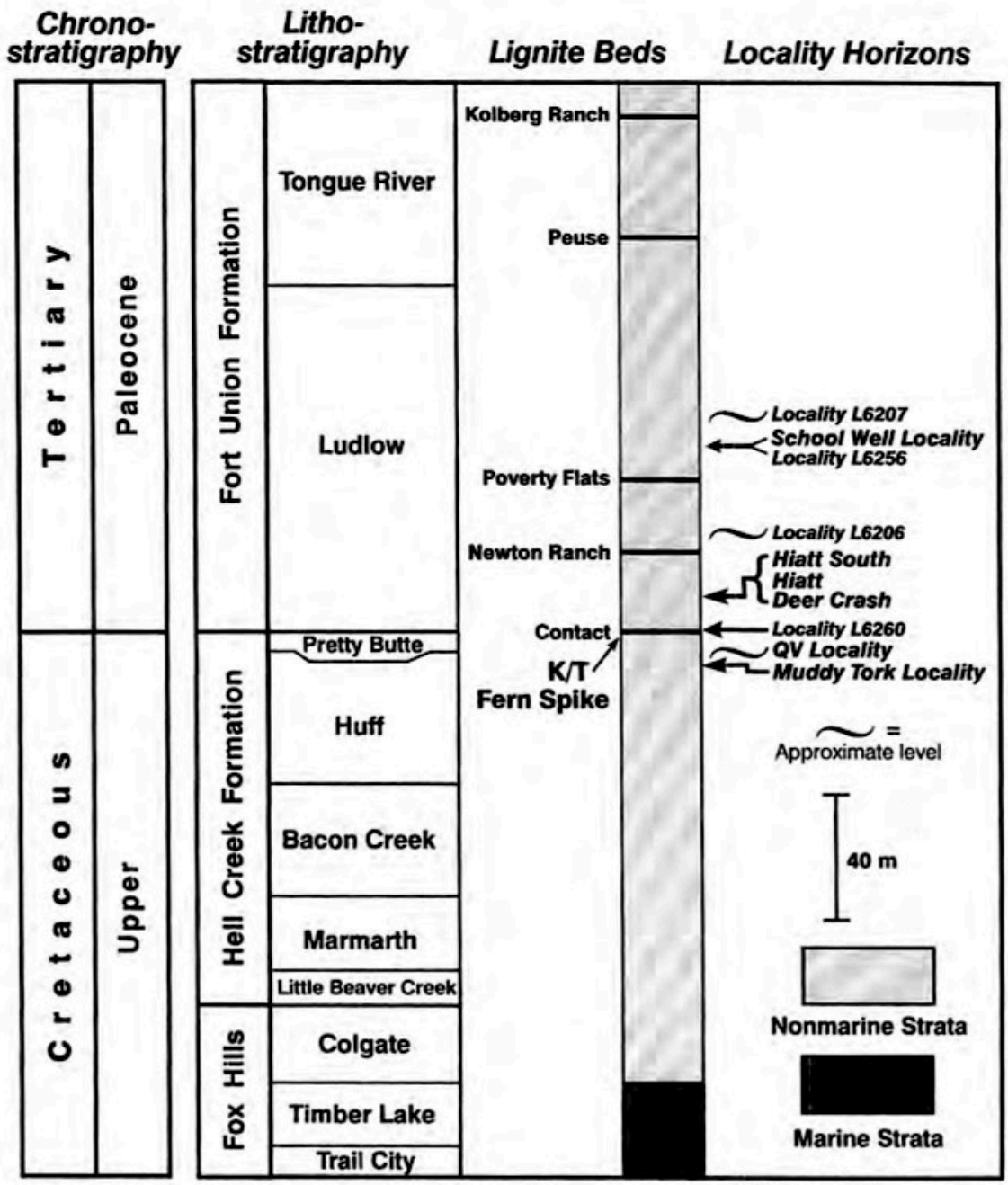


Figure 2. *This figure illustrates the general stratigraphy of the Glendive study area. Basic unit data were derived from Butler (1980), Sholes and others (1989), S. M. Vuke (written communications, 1994,1995), Daly (1991), and Hartman (unpublished observations). The placement of fossil localities and the fern spike were determined as part of Hunter et al (1997)(See also Kroeger and others, 1993). Mammalian localities are referred to by name. The figure was adapted from Hunter et al., 1997.*

2. Methods

i. Interproximal Wear Facets

Mammalian teeth are composed of two main calcified tissues, dentin and enamel. The enamel is a hard outer layer on the tooth under which lies the softer dentin. Throughout an individual's life, as it masticates, the surfaces of the teeth interact with each other and with the material being chewed. These actions cause slow but consistent wear on the enamel and through to the dentin. The wear creates planar surfaces known as wear facets, which can provide valuable insight into multiple aspects of an individual's life habits such as chewing pattern or diet.

Similar to wear facets formed through mastication, planar surfaces form between teeth called interproximal wear facets. The formation of interproximal wear facets is caused by slight jostling or movement that causes wear unique in size, shape and orientation for each tooth abutment. This means that the distal surface of one tooth and the mesial surface of the next will share a similar interproximal wear facet. This fact can be used to prove that two teeth, found individually, sat next to each other during life.

The School Well samples were not collected while still in the mandible, but were scattered. Because of this, the samples were closely inspected for the presence of interproximal wear facets to determine whether the samples did, in fact, belong to the same side of the lower dentition of a

single individual. Validation of the School Well samples relatedness would allow one to assess them as a single entity and identify them accordingly.

ii. Phylogenetic Analysis

Characterization of morphology to be used for comparison between individuals can prove to be difficult, especially when differences are very small. With the application of a coding strategy, the morphology of a given sample can be quantified and analyzed providing information about morphologic difference and relatedness between samples. For example, in the simplest form one would code "1" for the presence of a trait and "0" for its absence. Using an array of characters, analysis can be performed to determine the most parsimonious relationship between individuals based on their related traits. In order for analysis to provide a valuable level of resolution there must be a balance between the number of individuals characterized and the use of characters that provide significant distinction between lineages.

In studies of extant organisms the use of genomic traits allows for the use of thousands of unique characters, providing a much higher confidence of relatedness. However, when analyzing fossil organisms the number of quantifiable traits is much smaller and is limited to morphologic characteristics. This restricts paleontology to defining species based strictly on the morphological species concept. Interestingly, mammalian teeth can be used as species-specific identifiers.

In general mammalian teeth are represented by four main types of teeth; incisors, canines, premolars and molars. The incisors are used

primarily for food acquisition, grasping, nipping, stripping or scraping while canines are used for stabbing, biting, or holding prey. Premolars vary greatly amongst lineages and are used for crushing, slicing or shearing while the molars are used mainly to crush and grind food (Ungar, 2010). Each tooth serves a specific purpose, and tooth morphology varies greatly among both extinct and extant species, which can be attributed to differences in diet.

The lower molars of therian mammals can be separated into two portions, the trigonid and the talonid. The mesial portion of the tooth, the trigonid, generally sits higher than the talonid and contains the protoconid, paraconid and metaconid cusps. The talonid sits lower, lies distal to the trigonid and generally consists of the hypoconid and hypoconulid. (Figure 3)

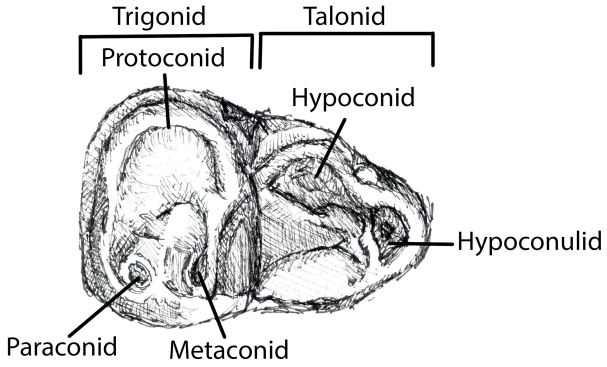


Figure 3. *This illustration, depicting the right third lower molar found at the School Well locality, highlights the placement and names of various cusps. Please note that not all of the cusps and features are labeled here.*

This study focuses on the family Hyopsodontidae, which lies within the order Condylarthra or archaic ungulates, which can be defined by three synapomorphic dental characteristics: teeth more bunodont with relatively

low cusp relief; lower molar trigonids shortened anteroposteriorly; and m3 with hypoconulid large and posteriorly projecting (Archibald, 1993).

Because mammalian tooth morphology varies so greatly among groups it is often possible to identify individuals to species level based strictly on dental features. With this technique, a set of fifty-nine characters previously used in publications by Zack et al. (2005) and Williamson and Weil (2011) were used to score the dental features of the School Well samples. Of the 59 characters, 28 of the characters were applicable to the School Well individual. The scores were then combined with the character-by-taxon matrix data used in the previous publications. The data were then processed using the phylogenetic program, TNT.

iii. Eruption Sequence, Maturation Rate, and Body Mass Estimation

The sequence of tooth eruption in fossil mammals can be estimated by comparing the relative amount of wear among teeth of a single individual. Regardless of the species, a tooth, once it has erupted, becomes available for use in for food acquisition or processing, and the tooth will begin to wear. The longer a tooth is erupted or exposed to use, the more wear that will accumulate. Based on the simple principle of relative wear accumulation over time the general sequence of tooth eruption can be estimated. Insofar as features of tooth eruption are functionally related to growth rates and aspects of life history in mammals, tooth eruption sequence can be utilized to predict these aspects in fossil mammals.

Based on the above principle of accumulated wear the School Well individual was examined, and the teeth were ranked in order of most to least wear. The School Well individual's teeth were inferred to have erupted in the order m1, m2, m3, p3 and p4, lacking information of the incisors. This eruption sequence was then compared to published information relating tooth eruption patterns with maturation rate and lifespan using ideas previously proposed by (Adolph Schultz, 1960).

"*Schultz's rule states that there is a tendency for replacing teeth to come in relatively early in slow-growing, longer-lived species.*" (Smith, 2000) This statement indicates that relative to the length of an individual's life, longer living animals replace their teeth earlier than those who have shorter

lifespans. “There can be little doubt that these ontogenetic specializations represent necessary adaptation to the gradual prolongation of the period of post-natal growth” (Schultz, 1960).

Similarly to the estimation of maturation rate, body mass is often estimated for fossil organisms to aid in reconstruction of aspects of a mammal’s biology. An individual’s body mass, when combined with other factors, can help one more completely describe its ecology. Using the surface area of the lower first molar, estimates of body mass can be made using standard least-squares regression to predict body mass (Legendre, 1986).

The body mass of the School Well individual was estimated using this the least squares method using parameters that have been published previously by Legendre (1986), which were established using seven faunal samples inclusive of 58 species. The genus *Tupaia,* which was used for comparison of eruption sequence, was represented by an individual belonging to *Tupaia glis* (Fish, 1983). The individual was used to check the precision of the method proposed by Legedre, 1986. The parameters for small mammals that are less than 500g and the following formula was used.

$$\mathbf{\ln X = a \ln Y + \ln b}$$

X= Body Weight; **Y**= m1 Crown Area (Length x Width, in mm); **a**= Slope; **ln b**=Intercept

Parameters for individuals < 500g: Slope (a)= 1.621; Intercept (Ln b)= 1.786; Correlation coefficient= 0.885.

iv. Image Capture & Editing

Initial images of the samples were created manually using a microscope attachment called a camera lucida. This device allows an individual to view a specimen under the microscope while simultaneously viewing a separate surface where the object can be "traced" or drawn. Figure 3 was created utilizing this method, which allowed for a general depiction of the samples. This method does however allow for human error and the reliability of depiction depends heavily on the skill of the artist.

The Hirox digital microscope is a computerized unit useful in taking well-focused images with semi-automated image stacking. The Hirox has a relatively small resolution sensor so the quality of the images produced is limited. However the Hirox serves as a valuable tool in producing very accurate 2D measurements, which was utilized for the measurement of the School Well samples for literature comparison.

For large, high-quality image capture a Wild binocular microscope with a DSLR photo diaphragm attachment was used. A Cannon EOS was attached via the attachment allowing for remote capture using EOS utility for the Macintosh. This method allows for a higher level of control of image lighting in addition to producing very high quality images. The images captured were then processed and edited using Adobe Photoshop.

3. Results

i. Interproximal Wear Facets

When the School Well Samples were originally collected by Dr. John Hunter they were gathered from the surface within less than a square meter of each other. One could assume that the samples belonged to the same individual. However, in order to reject the possibility that the specimens belong to multiple individuals, a close inspection of the interproximal wear facets was undertaken. Fortunately, the School Well individual lived long enough to form significant interproximal wear facets that could easily be identified and used as identifiers specific to each tooth abutment.

Through this assessment, similar interproximal wear facets were found between the distal p3 and the mesial p4 (Figure 4), the distal p4 and the mesial m1 (Figure 5), and the distal m2 and mesial m3 (Figure 6). The absence of the trigonid of the m2 prevented the assessment of the interproximal wear facet between the distal m1 and the mesial m2. Although the m1 and m2 could not be directly related by means of this assessment, the relatedness of the samples is highly likely based on the proven relationship amongst the other samples combined with the fact they were found within reasonable proximity to each other. Based on this conclusion the School Well samples are referred to as the School Well individual.

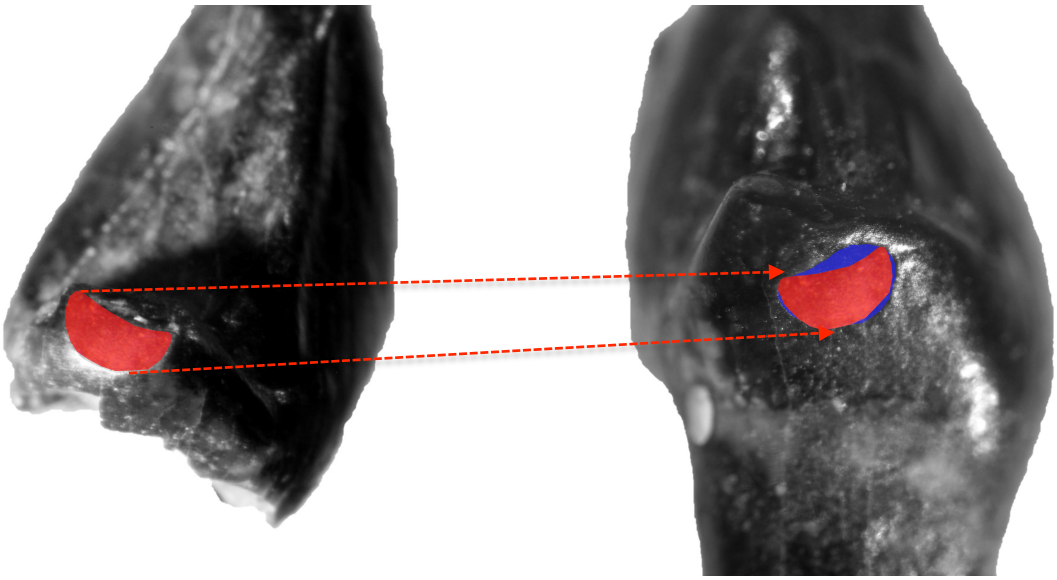


Figure 4. *An image depicting the interproximal wear of the distal p3 highlighted in red. A mirror image of the p4 is shown with the mesial interproximal wear facet hightlighed in blue. The distal p3 facet was then slightly rotated and superimposed on that of the mesial p4.*

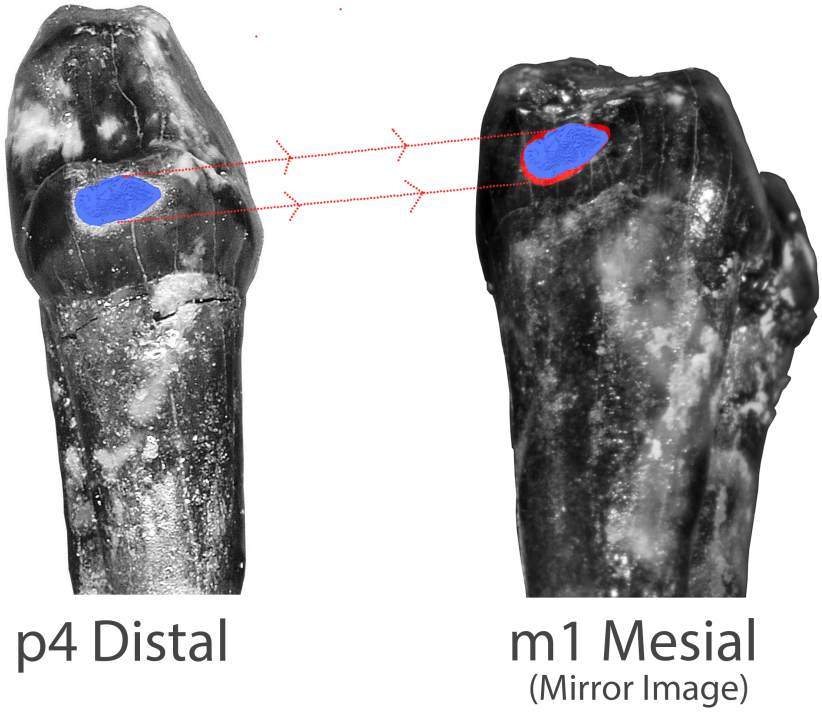


Figure 5. *An image depicting the intrerproximal wear of the distal p4 highlighted in blue. A mirror image of the m1 is shown with the mesial interproximal wear facet highlighted in red. The distal p4 facet was then superimposed on that of the mesial m1.*

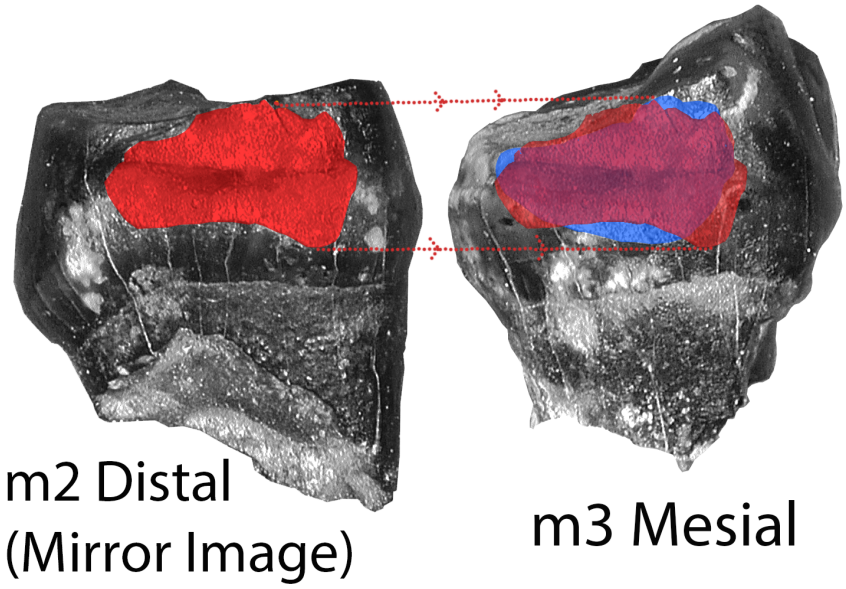


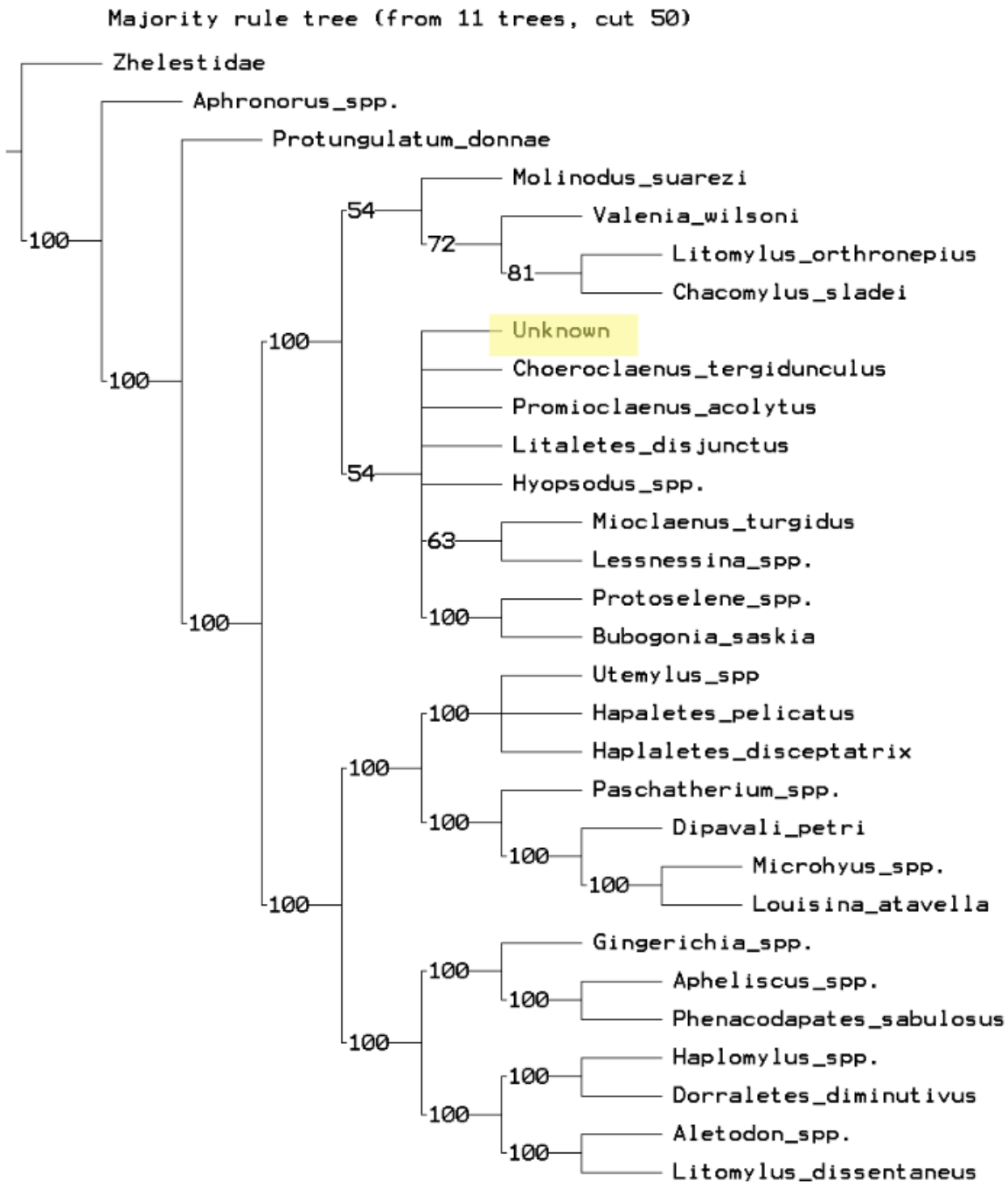
Figure 6. *An image depicting the interproximal wear of the distal m2 highlighted in red. A mirror image of the m3 is shown with the mesial interproximal wear facet highlighted in blue. The distal m2 facet was then superimposed on that of the m3.*

ii. Phylogenetic Analysis

Due to a sufficient number of characteristics relevant to the School Well individual the coding scheme previously published by Zack et al. (2005) and Williamson & Weil (2011) proved to be a valuable tool in gathering an initial assessment of the classification of the School Well individual. Zack et al. (2005) characterized the best-known representatives of Hyopsodontidae including Mioclaeninae, which span multiple families including both Hyopsodontidae and the basal Apheliscinae. The data were processed producing the eleven most parsimonious trees, which were then combined into a majority rule or consensus tree. (Figure 7)

The analysis placed the School Well individual within the family Hyopsodontidae and further within the subfamily of Mioclaeninae. Unfortunately, the consensus tree provides little resolution amongst individuals within Mioclaeninae. A character-by-taxon matrix more specific to Mioclaeninae could eliminate this issue and would prove valuable in the identification of the School Well individual but is not within the scope of this project. Nonetheless, the outcome of the phylogenetic analysis verifies the preliminary assessment made by Dr. John P. Hunter, who suggested the School Well individual may belong to the genus Promioclaenus or a related taxon. The analysis identifies the School Well individual as a member Mioclaeninae, which is inclusive of the genus Promioclaenus.

Figure 7. *Phylogenetic relationship of "hyopsodontids," mioclaenids and Aphronorus. The School Well individual is represented by the yellow, "Unknown".*



iii. Eruption Sequence and Body Mass Estimation

The eruption sequence estimated by relative wear was then compared to the eruption sequence of extant species that have been previously analyzed. It was found that the School Well individual shares a common eruption sequence generalized for fast-growing (See Figure 8), quickly maturing eutherian mammals such as *Tupaia* (Treeshrew), which matures in as little as five weeks. During the early radiation of mammals long lifespan and slow maturation were probably uncommon (Smith, 2000).

Because *Tupaia glis* exhibits an eruption sequence similar to that of the School Well individual it serves as an acceptable modern day correlate, allowing other predictions of life history to be made. With parameters proposed by Legendre (1986), the body mass of the School Well individual was first estimated using the surface area of the first lower molar and found to be 488.33 grams (1.076 lbs). This predicted body mass could then be applied to various proposed regressions to predict basal metabolic rate (Hayssen and Lacy, 1985), growth rate (Millar, 1977), gestation period and litter size (Miller, 1981).

Based on these calculations one can predict that the School Well individual was a small, fast-growing mammal weighing roughly 488 grams. The individual had a gestation period of roughly 53 days and had litters of between three and four offspring that grew at a rate of 2.86 grams per day. The adult basal metabolic rate was estimated to be 6226.32 Joules per hour.

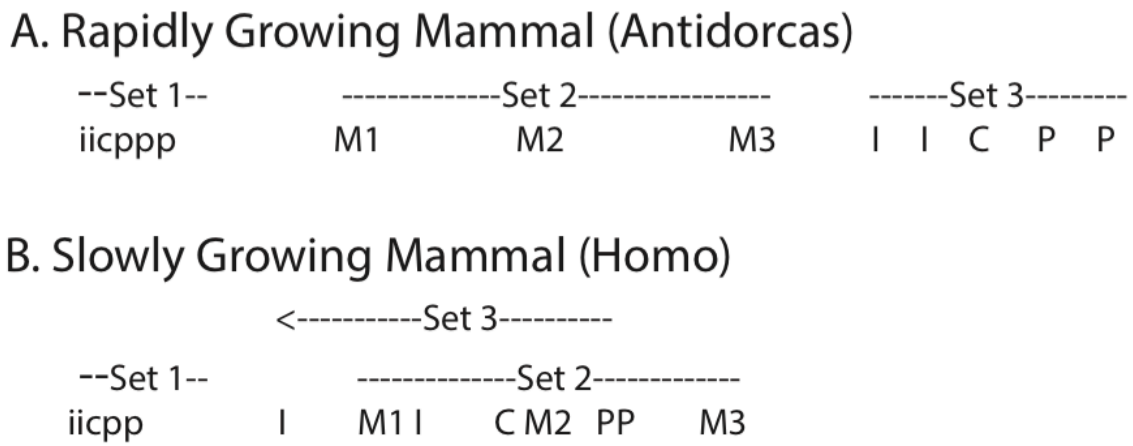


Figure 8. *Illustrates the sequence of eruption of tooth eruption in fast and slow growing mammals. M=Molar; I=Incisor; P=Premolar. Lower case letters represent deciduous or "Baby" teeth.*

4. Systematic Paleontology

Family Hyopsodontidae Trouessart, 1879
Genus *Promioclaenus* Trouessart, 1904

Promioclaenus sp. cf. P. acolytus

i. Diagnosis

The School Well individual differs from all other species of Promioclaenus except for *P. acolytus (= P. aquilonius, E. aquilonius).* The School Well individual differs from *P. acolytus* by lacking a pronounced hypoconulid on the distal m1 as well as lacking distinctive labial cinguli on the m1-3. The latter could possibly be contributed to the extent of wear and weathering on the School Well samples. The size of the School Well samples closely resembles that of known measurements of *P. acolytus*. In addition both the School Well individual and *P. acolytus* have a p4 with a distinct paraconid as well as a rudimentary metacone lying on the protocone.

Specimens

All measurements are presented in millimeters. MOR 815e, right p3 (Lg=3.648, W= 2.143); MOR 815d, right p4 (L= 4.353, W= 2.686); MOR815b, right m1 (L= 4.343, W=3.486); MOR 815c, right m2 talonid (W=3.358); MOR 815a, right m3 (L=4.301, W=2.938). Refer to Figures 9-11 for labial, lingual and occlusal views.

ii. Description

p3: The p3 is partially fractured so the mesial end of the tooth could not be described. The protoconid is relatively uninflated without the presence of any secondary cusps. The talonid consists of one lunate cusp that meets the trigonid at an angular "v" that is the talonid basin, which is opens both labially and lingually.

p4: The p4 is relatively more inflated than the p3 and is more molaraform. There is a precingulid that wraps slightly around the labial protoconid. There is a distinct paraconid that lies mesiolingual to the protoconid. There is a rudimentary metaconid that sits distolingual to the protoconid. An entoconid and a slightly larger hypoconid form a relatively basinal talonid.

m1: The trigonid of the m1 is roughly the same size as the talonid and has a precingulid wrapping around the protoconid, paraconid, and metaconid. The paraconid and metaconid sit at relatively the same height and are roughly equal in size. The protoconid is heavily worn but is rounded and extends labially. The talonid sits only slightly lower than the trigonid, and the entoconid is the most inflated of the cusps. There is a very small entoconulid that sits mesial to the entoconid. The hypoconid is intermediately rounded and extends only slightly distolabial. The hypoconulid is very reduced and leads to a postcingulid that wraps around the labial side of the hypoconid.

m2: The m2 is a partial sample represented by only the talonid. The hypoconid is the dominant cusp that extends only slightly distolabially. The entoconid is relatively small and round, and not inflated. The hypoconulid is larger than seen in the m1 and extends slightly more distally but remains the smallest cusp. It however does continue to a small postcingulid that does not wrap around the hypoconid as in the m1.

m3: The m3 has the strongest precingulid of all of the samples wrapping around the protoconid, paraconid and the metaconid. The paraconid and metaconid are mesiodistally compressed but are not fused. The metaconid is dominant over the paraconid, but both cusps are relatively uninflated. The protoconid is heavily worn but is relatively large and rounded, and extended directly labially. The talondid is elongate and substantially basinal. The hypoconid is rounded, slightly inflated and extends labially. The entoconid is present but is neither enlarged nor reduced. The hypoconulid is slightly rounded and extends distally.

Figure 9. *Labial view images of the School Well samples. A. p3; B. p4; C. m1; D. m2; E. m3. Note: Samples are not to scale and do not represent size relations to each other.*

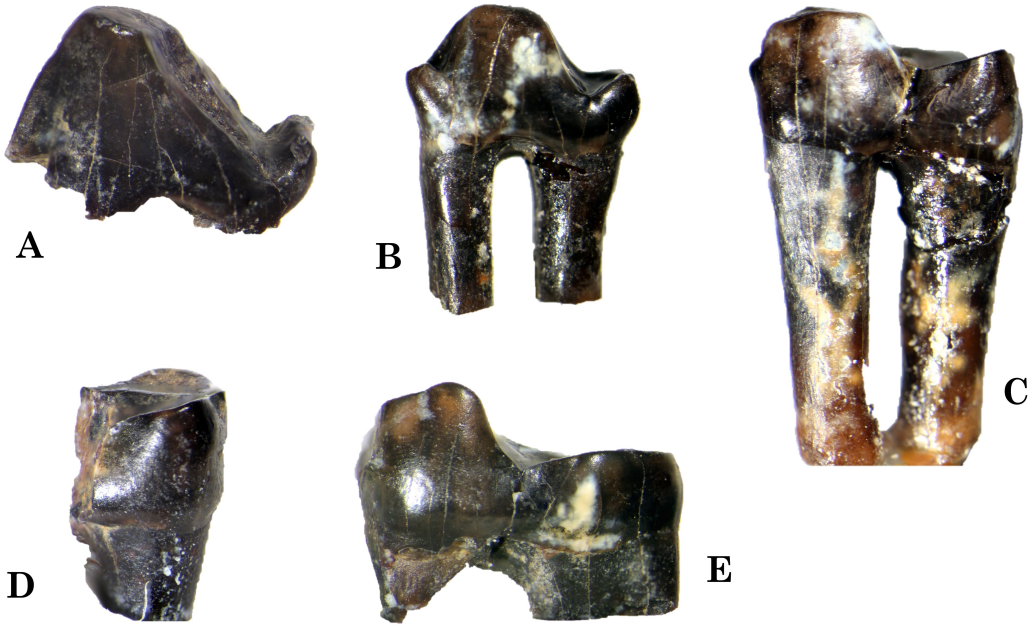


Figure 10. *Lingual view images of the correlated School Well samples. A. p3; B. p4; C. m1; D. m2; E. m3. Note: Samples are not to scale and do not represent size relations to each other.*

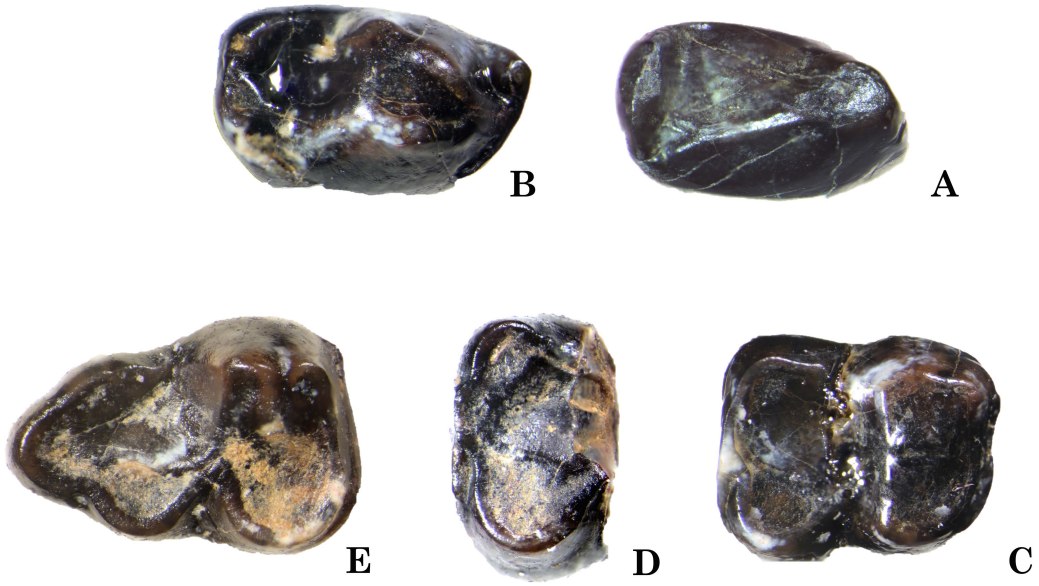


Figure 11. *Occlusal view images of the correlated School Well samples. A. p3; B. p4; C. m1; D. m2; E. m3. Note: Samples are not to scale and do not represent size relations to each other.*

iv. Comments

With the conclusion that the School Well individual falls within the family Hyopsodontidae based on phylogenetic analysis and a direct morphological comparison (See Appendix 3), further investigation was done to identify the individual to the genus and species level. The organization of this group is historically scattered, and "*Hyopsodontidae* served as a wastebasket taxon for "generally small, primitive ungulates not clearly specialized enough to warrant allocation to other, more advanced supragenetic groups."" (Cifelli 1983)

While the School Well individual has confidently been identified as a species comparable to *Promioclaenus acolytus*, the accurate placement of this and other species within the genus Promioclaenus is questionable. The genus Promioclaenus was first proposed by Édouard Louis Trouessart in 1904 and was later supported by David Archibald in the 1998 publication of *Evolution of Tertiary Mammals of North America. Volume 1* (Janis et al., 1998). This definition was used by Scott et al. (2013) in the addition of a new member of the genus Promioclaenus, *Promioclaenus thnetus.*

According to Archibald (1998) affirmed definition of the genus Promioclaenus the "P4/p4 is without a distinct paraconid". (See Appendix 3 for full description) In consequence, the presence of a distinct paraconid lying mesiolingual to the protoconid of the p4 the School Well individual should prevent it from being placed within the genus Promioclaenus. In addition,

Scott et al. (2013) also describe *P. thnetus* as "having a better-developed paraconid on the p4", which should also prevent it from being placed within Promioclaenus.

Van Valen (1978), added a new species to the genus Promioclaenus, *Promioclaenus wilsoni.* The described specimens were poorly preserved and were not represented by adequate lower dentition. The specimens were then reevaluated by Muizon (2000), and the conclusion was reached that the specimens should be placed within their own new genus, Valenia, thus reassigning *"P." wilsoni* to *Valenia wilsoni.* Through this example it is easy to see how the primitive morphology of condylarths makes different allocations defensible depending on emphasized characters (Rose, 2006).

According to current defining features two members of Promioclaenus, *P. thnetus* and *P. acolytus,* should not be placed within the genus. An alternate placement of the individuals was explored throughout this project without resolution. A closer analysis and reorganization of individuals within the subfamily Mioclaeninae and a redefining of Promioclaenus could be necessary to properly assess the proposed contradiction.

5. Discussion

There is a general trend in condylarth evolution for the cusps of the teeth to become shortened in height and the premolars moving toward becoming more inflated and molariform. Although the School Well condylarth has been identified as a species that is comparable to *Promioclaenus acolytus*, it differs morphologically most noticeably by the above average length of the premolars, more specifically the p4. The School Well individual has a p4 that is nearly the exact length as its m1, suggesting the individual belongs to a group further developed with more derived characteristics.

The majority of faunas that contain individuals belonging to *Promioclaenus acolytus* come from localities in New Mexico and Wyoming with a heavy concentration in the late Torrejonian (To2-3). The species *Promioclaenus thnetus* was recently named in Alberta in the middle Torrejonian (To2) Deathwish locality, simultaneously occurring with many positively identified instances of *P. acolytes* elsewhere. This suggests spatial variation within the genus and brings into question the species *P.acolytus,* which consists of individuals that were originally placed in *Promioclaenus aquilonius* and *Ellipsodon aquilonious*. With the School Well locality lying between New Mexico and Alberta one might suggest that the School Well individual belonged to a group that was spatially separate from both the individuals in the southwestern United States and those of western Canada.

A reevaluation of the members of the currently defined *Promioclaenus acolytus* could reveal that the *Promioclaenus acolytus* actually consists of a spectrum of individuals varying by geographic distribution.

The School Well local fauna currently include *Ptilodus montanus, Paromomys maturas, Litaletes c.f.L. mantiensis* and *Periptichus sp.* (Hunter et al., 1997). Based on known temporal distribution of these species the School Well fauna suggests that the locality occurs within the early to middle Torrejonian biochron but cannot be further constrained. The identification of the School Well individual as *Promioclaenus sp. cf. acolytus* allows this taxon to be added to the School Well local fauna as well as adds to the the temporal information of the locality. However, this addition cannot further constrain the Locality to a specific biochron but is in support of the original assessment of the age of the School Well locality as early Torrejonian.

6. Conclusions

Through the investigation of interproximal wear facets the samples collected at the School Well locality were found to belong to a single individual. Characterization and phylogenetic analysis allowed for an initial assessment placing the individual within the family Hyopsodontidae and further within the subfamily Mioclaeninae. After direct comparisons with known specimens, it was concluded that the School Well individual belongs to a species comparable to *Promioclaenus acolytus*. Life history of the individual was predicted by first estimating the individuals body mass which was then used to explore multiple factors of its paleobiology including metabolic rate, gestation time, litter size as well as growth rate. While the information gathered allows insight into the individual's life history, the addition to the School Well local fauna does not allow for the locality to be positively constrained to a specific biochron.

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8. Appendices

i. Character State Definitions and Symbols.

1. p4 subequal to m1 or somewhat smaller (0) or markedly larger than m1 (1).

2. p4 paraconid better developed than metaconid (0), as developed as metaconid (1), or weaker than metaconid (2). Ordered.

3. p4 trigonid anteroposteriorly short and high crowned (0) or elongate and low crowned(1).

4. p4 protoconid uninflated or weakly inflated (0), moderately inflated (1), or strongly inflated (2). Ordered.

5. p4 talonid anteroposteriorly elongate (0) or abbreviated antero–posteriorly (1).

6. p4 cristid obliqua contacts back of trigonid at level of notch between protoconid and metaconid (0), more buccally beneath posterior protoconid crest (1), or cristid obliqua absent (2).

7. p4 talonid basined (0) or unbasined (1).

8. Distention of enamel on buccal side of lower molars absent (0), weak (1), or strong (2). Ordered.

9. Lower molar trigonids much higher than talonids (0), somewhat higher than talonids (1), or trigonids and talonids subequal in height (2). Ordered.

10. m1–3 buccal cingulid absent or weak and restricted to hypoflexid (0) or strong and complete at least around the trigonid (1).

11. m1–2 talonids broader than trigonids (0), trigonids and talonids subequal in width (1), or trigonids broader than talonids (2). Or–dered.

12. m1–3 paraconids tall relative to protoconids and metaconids (0) or low (1).

13. m2–3 paraconid distinctly separated from metaconid (0) or par– tially to completely fused to metaconid at base (1).

14. Paraconid on m1–3 positioned at lingual margin of crown (0) or between protoconid and metaconid (1).

14. Molar paracristid present and well developed (0) or weak to absent (1).

16. m1–3 metaconid inflated, size subequal to protoconid (0) or uninflated and smaller than protoconid (1).

17. m2 cristid obliqua orientation nearly parallel to anteroposterior axis of crown (0) or oriented around 45 degrees to long axis of crown (1).

18. m1–3 hypoconid much larger than other talonid cusps (0) or re− duced in size, smaller than entoconid (1).

19. Hypoconulid on m1–2 on lingual side of talonid, twinned with entoconid (0), in a median position, separate from hypoconid and entoconid (1), or shifted buccally and twinned with hypo− conid (2). Ordered.

20. Hypoconulid on m1–2 much smaller than entoconid and hypoconid (0), slightly smaller than entoconid and hypoconid (1), or larger than entoconid, slightly smaller than hypoconid (2). Ordered.

21. Notch in postentocristid between hypoconulid and entoconid on m1–2 present (0) or absent (1).

22. m1–2 entoconulid absent or very weakly developed (0) or well−developed (1).

23. m1–2 entocristid present and ascends posterior slope of metaconid to close talonid (0), present and wraps around, but does not ascend the base of the metaconid (1), or present and terminates at the base of the entoconid (2), or extremely faint to absent (3).

24. m2 entoconid taller than hypoconid (0), subequal in height to hypoconid (1), or lower than hypoconid (2). Ordered.

25. m3 trigonid width subequal to or slightly wider than m2 trigonid width (0), somewhat narrower than m2 trigonid width (1), or much narrower than m2 trigonid width (2). Ordered.

26. m3 talonid narrower than m3 trigonid (0) or subequal to trigonid width (1).

27. m3 talonid elongate (0) or anteroposteriorly compressed (1).

28. P4 parastyle present and relatively well−developed (0) or weak to absent (1).

29. P4 metacone absent (0), weakly developed (1), or well devel− oped and well separated from paracone (2). Ordered.

30. P4 protocone much smaller than paracone (0) or slightly smaller than to subequal to paracone (1).

31. P4 preprotocrista complete between protocone and parastyle, interrupts anterior cingulum (0) or incomplete such that the an− terior cingulum continues to parastyle uninterrupted (1).

32. P4 postprotocrista complete between protocone and metastyle, interrupts posterior cingulum (0) or incomplete such that the posterior cingulum continues to metastyle uninterrupted (1).

33. P4 hypocone absent (0) or present (1).

34. M1–2 paracone subequal in size to metacone (0) or larger than metacone (1).

35. M1–2 mesostyle absent (0) or present (1).

36. Ends of postparacrista and premetacrista on M1–2 aligned (0) or anterior end of premetacrista terminates buccal to posterior end of postparacrista(1).

37. M1–2 preparaconule crista complete from paraconule to para−style, anterior cingulum terminates against preparaconule crista (0) or preparaconule crista incomplete, anterior cingulum con− tinues to parastyle (1).

38. M1–2 postmetaconule crista complete from metaconule to meta− style, posterior cingulum terminates against postmetaconule crista (0) or postmetaconule crista incomplete, posterior cingulum con− tinues to metastyle (1).

39. M1–2 metaconule equidistant between buccal and lingual cusps (0) or shifted lingually, nearly in line with protocone and hypo− cone (1).

40. M1–2 protocone greatly enlarged relative to paracone and meta− cone (0), larger, but not considerably larger, than paracone and metacone (1), or subequal to or smaller than paracone and metacone (2). Ordered.

41. M1–2 postprotocrista present (0) or absent (1).

42. M1–2 postprotocingulum absent (0) or present (1).

43. M1–2 hypocone small to absent (0), well developed but smaller than

protocone (1), or subequal in size to protocone (2). Ordered.

44. M1–2 pericone absent (0) or present (1).

45. M1–2 posterior cingulum arises from same level on protocone as anterior cingulum (0) or arises higher on protocone than anterior cingulum (1).

46. Calcaneal tuber short relative to body of calcaneum (0) or rela– tively elongate (1).

47. Fibular facet on calcaneum absent (0), present and relatively flat (1), or present and strongly curved to parallel the curvature of the astragalar trochlea (2). Ordered.

48. Long axis of ectal facet on calcaneum subparallel to long axis of calcaneum (0), approximately 45 degrees to long axis of calca– neum (1), or nearly perpendicular to long axis of calcaneum (2). Ordered.

49. Calcaneal ectal facet nearly flat, with a large radius of curvature (0), more strongly curved, with a smaller radius of curvature (1), or sharply divided into a medially facing posterior surface and an anteriorly facing anterior surface (2). Ordered.

50. Peroneal tubercle anteroposteriorly short (0) or elongate (1).

51. Medial trochlear ridge of astragalus absent such that medial por– tion of trochlea faces dorsomedially (0) or present such that me– dial portion faces medially (1).

52. Trochlear groove on astragalus shallow (0) or deep (1).

53. Radius of curvature of lateral trochlear ridge of astragalus greater than that of medial ridge (0) or subequal to radius of medial ridge (1).

54. Astragalar foramen present (0) or absent (1).

55. Trochlear articular surface only extends onto posterior surface of astragalus medially (0) or articular surface extends onto posterior surface across width of trochlea (1).

56. Cotylar fossa on astragalus weak or absent (0), prominent and primarily dorsally oriented (1), or prominent and medially oriented (2). Ordered.

57. Lateral process on astragalar body formed by lateral projection of ectal facet absent (0) or present (1).

58. Posteromedial projection of astragalar body absent (0) or present (1).

59. Long axis of navicular facet of astragalus oriented transversely or more parasagittally (1).

ii. Character-by-taxon matrix

Character-by-taxon matrix used by Scott et al. (2013)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Zhelestidae	0	2	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	?	0	0	0	1	1
Protungulatum donnae	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0	0	0	0
Bubogonia saskia	?	?	?	?	?	?	?	0	1	1	1	0	1	0	0	0	1	0	0	1	0	1	2	2	1	1	0	?	?	?
Protoselene spp.	0	0	0	1	0	1	0	0	1	0	1	0	(0,1)	1	0	0	1	0	0	1	0	(0,1)	2	2	1	1	0	0	1	1
Hyopsodus spp.	0	1	0	0	0	1	0	0	2	0	1	0	1	0	0	0	1	0	0	1	0	(0,1)	2	1	0	1	0	0	0	1
Litaletes disjunctus	0	1	0	0	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	1	1	1	2	2	1	0	0	0	(0,1)	1
Lessnessina spp.	0	1	0	0	0	1	0	0	1	1	1	0	1	0	0	0	0	0	1	1	1	(0,1)	2	2	0	0	(0,1)	0	0	1
Promioclaenus acolytus	0	1	0	1	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	1	1	1	2	1	1	0	0	0	0	1
Choeroclaenus turgidunculus	0	–	0	1	1	–	–	0	1	0	1	0	1	0	0	0	1	0	0	2	1	1	2	1	1	0	0	1	0	1
Mioclaenus turgidus	1	–	0	2	1	–	–	0	1	0	2	0	1	0	0	0	0	0	0	2	1	–	0	2	2	0	0	0	0	1
Molinodus suarezi	?	2	0	0	0	0	0	0	1	(0,1)	2	0	1	0	0	0	1	0	0	2	1	0	3	1	1	0	0	0	0	1
Paschatherium spp.	0	2	0	0	0	2	0	1	0	0	2	1	0	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	2	1
Dipavali petri	0	2	1	1	0	0	0	0	1	0	2	1	0	1	0	1	0	1	2	0	0	0	0	0	2	0	1	?	?	?
Louisina atavella	0	2	0	0	0	0	0	1	1	0	2	1	0	1	0	1	0	1	2	0	0	0	2	0	2	0	1	1	2	0
Louisina mirabilis	0	2	0	0	0	0	0	1	1	0	2	1	0	1	0	1	0	1	2	0	0	?	?	?	2	0	1	?	?	?
Microhyus spp.	0	–	0	0	0	–	–	2	2	0	1	1	0	–	1	1	0	1	2	0	0	1	2	0	2	0	1	1	2	1
Litomylus dissentaneus	0	1	1	0	1	1	0	0	1	(0,1)	1	1	0	1	0	0	1	0	0	1	0	0	2	1	0	0	0	0	0	1
Aletodon spp.	1	1	1	0	1	1	0	0	2	0	1	1	0	1	1	0	1	0	1	1	0	0	2	1	1	0	0	0	0	1
Gingerichia spp.	1	–	0	1	1	–	–	1	1	0	1	1	0	1	0	0	1	0	0	1	0	0	2	1	1	0	0	1	0	0
Phenacodaptes sabulosus	1	1	0	1	0	0	1	0	1	0	1	1	0	1	1	0	0	0	0	1	0	0	2	1	1	0	0	1	0	0
Apheliscus spp.	1	–	0	0	0	1	1	0	1	0	1	1	0	–	1	0	0	0	0	1	0	0	2	1	0	1	0	1	0	0
Haplaletes disceptatrix	0	1	1	0	0	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1
Dorraletes diminutivus	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	0	1	?	0	?	1	1	0	0	0	1	1
Haplomylus spp.	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	0	1	1	0	2	1	1	0	0	0	1	1
Haplaletes pelicatus	0	1	0	1	0	0	0	1	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	?	?	?
Utemylus spp.	?	–	0	2	1	–	–	2	1	0	1	1	0	1	0	0	1	0	0	0	–	1	0	0	0	0	0	0	0	1
Aphronorus spp.	1	2	0	1	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	0	2	1	0	1	0	1	0	1

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
Zhelestidae	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Protungulatum donnae	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	1
Bubogonia saskia	?	?	?	?	0	?	?	?	0	1	0	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Protoselene spp.	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hyopsodus spp.	1	0	0	0	0	0	0	1	0	1	0	0	1	1	1	0	1	1	1	0	0	0	1	0	0	0	0	1	0
Litaletes disjunctus	1	0	0	0	0	1	1	1	0	1	0	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lessnessina spp.	1	0	0	1	1	?	1	1	0	1	0	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Promioclaenus acolytus	1	1	0	1	0	0	1	1	0	1	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Choeroclaenus turgidunculus	–	–	0	1	0	0	0	0	0	1	0	0	0	0	1	?	?	?	?	?	0	0	1	0	0	0	1	1	1
Mioclaenus turgidus	–	–	0	1	1	?	1	1	0	0	1	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Molinodus suarezi	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	2	2	0	1	0	0	–	0	0	0	0	1	0
Paschatherium spp.	0	0	1	1	0	0	0	(0,1)	0	2	0	0	1	0	0	1	0	1	1	1	1	1	0	1	1	1	0	0	1
Dipavali petri	?	?	?	1	0	0	0	1	0	2	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Louisina atavella	0	1	1	1	0	0	1	1	1	2	0	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Louisina mirabilis	?	?	?	1	0	?	1	1	1	2	0	0	2	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Microhyus spp.	1	1	1	1	0	0	1	1	1	1	1	0	2	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Litomylus dissentaneus	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aletodon spp.	?	?	0	0	0	0	(0,1)	1	0	1	0	(0,1)	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gingerichia geoteretes	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Phenacodaptes sabulosus	0	0	0	1	0	1	1	1	0	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apheliscus spp.	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	1	2	2	0	0	1	1	0	1	1	1	0	0	1
Haplaletes disceptatrix	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dorraletes diminutivus	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplomylus spp.	1	1	0	0	0	0	0	1	0	1	0	1	0	1	–	1	2	2	2	0	1	1	1	1	1	2	1	0	1
Haplaletes pelicatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Utemylus spp.	1	0	0	0	0	0	1	1	0	1	0	1	0	0	–	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aphronorus spp.	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Character-by-taxon matrix from Williamson and Weil (2011) with addition of the School Well individual.

	10	20	30	40	50	60
Chacomylus sladei	???????110	1010001001	1021100110	0?000??001	01101?????	?????????
Litomylus orthronepius	???????110	1010001011	1021100???	???0000001	01100?????	?????????
Valenia wilsoni	0200000010	1010001011	1021100011	0000000001	01000?????	?????????
Unknown	02100?1110	101000-000	-?32000???	??????????	??????????	?????????

iii. Definitions and Comparisons

Detailed definitions and comparisons used in the study of the School Well individual.

Definitions

Order Condylarthra (Archaic Ungulates)

Prothero, et al. (1988) cited three dental characters that are presumably synapomorphic for ungulates: teeth with more bunodont with relatively low cusp relief; lower molar trigonids shortened anteroposteriorly; and m3 with hypoconulid large and posteriorly projecting.

Family Hyopsodontidae; Trouessart, 1879

Characteristics:

P4/p4 not inflated, generally moderate in size, cuspidate, somewhat molariform but never exactly so, p4 generally with a metaconid and wide but imperfect talonid basin. Molar paraconids median to subinternal, not fusing with metaconids, entoconids distinct and high, talonid basins closed. M3/m3 little or not reduced. M1-2 with definite hypocone, small in earlier and large in later forms, sharply distinct from tip of protocone (Simpson's 1937 definition of Hyopsodontinae).

Genus Promioclaenus; Trouessart, 1904

Characteristics:

P4/p4 cuspidate, more of less enlarged, but not really inflated. The p4 without distinct paraconid, metaconid absent or rudimentary, protoconid inflated rather than bladelike; talonid basined and relatively large. Molar hypocones weak, metaconules present. Molar trigonids with paraconids internal, fusing with metaconid; moderately separated metaconids and protoconids. Molar talonids with relatively wide basins, entoconids generally indistinct and fusing with hypoconulids (especially on m2) . M3/m3 moderatly reduced. M3 with reduced metacone. Rami relatively long and slender (Wilson, 1956, p.115).

Detailed Comparisons

All measurements presented are in millimeters.

Promioclaenus thnetus

In general the length of the S.W. samples is longer than those compared to the sample described by Scott et al. (2013). The School Well samples appear less inflated than those of *Promioclaenus thnetus* differing most obviously by the lack of a pronounced labial cingulum which is present on the p4-m3 of *P. thnetus*

p3: MOR 815e is incomplete mesially and so presence of a paraconid cannot be determined like that expressed by P. thnetus. MOR 815e appears to be only slightly less inflated than P.thnetus.

p4: The most similar tooth between the two individuals. The positioning of cusps is very similar with the presence of a paraconid mesiolingual to the protoconid. In both individuals there appear to be two small cusps on a more pronounced cusp distal from the protoconid. The metaconid on the distal buccal portion of the protoconid of MOR 815d is rudimentary or heavily worn while P.thnetus shows a more pronounced metaconid connected by a protocristid.

m1: The metaconid and paraconid in MOR 815b are more closely fused than seen in *P. thnetus*. The precingulum of *P. thnetus* is much more pronounced than seen in MORE 815b. *P. thnetus* has a bulbous cusp lying distal to the metaconid, which is absent in MOR 815b. The entoconid of *P.thnetus* extends more distally compared to MOR815b, which extends more labially. The hypoconulid is much more pronounced in *P. thnetus* compared to that of MOR 815b.

m2: Again, MOR 815c is more inflated than that of *P. thnetus*. There appears to be formation of secondary cusps on the hypoconid and entoconid of *P. thnetus* while MOR 815c shows little evidence of any secondary cusps, which could be attributed to the heavy wear on MOR 815c. The hyoconulid of *P. thnetus* is much more pronounced than seen in MOR 815c.

m3: The transition between the buccal and lingual sides of the trigonid is much more pronounced in *P. thnetus*. MOR 815a exhibits an inflated round protoconid while P. thnetus exhibits less inflation and the formation of an accessory cusp mesially. Wear patterns present on both individuals on in the talondid (mesial entoconid) indicate similar chewing patterns.

Promioclaenus, lemuroides

m2: The talonid of both *P. lemuroides* and the School Well individual are similar in several ways. The positioning of the hypoconid, hypoconulid and

the entoconulid are all located in very similar locations. The entoconid of the School Well individual is much more exaggerated than that of *P. lemuroides*. The School Well individual's hypoconulid is much more pronounced than that of *P. lemuroides*.

m3: Both the School Well individual and *P. lemuroides* have a precingulid on the mesial portion on the trigonid, but that of *P. lemuroides* is much stronger. Also similar to *P. lemuroides* the metaconid is strongly dominant over the paraconid, however the metaconid and paraconid have become mesio-distally compressed in the School Well individual. *P. lemuroides* paraconid and metaconid have much more separation than MOR 815a. The protoconid of the School Well individual is much more round and extends labially, while that of *P. lemuroides* extends more distally. The hypoconid of the School Well individual is very near the junction of the trigonid and talonid while that of *P. lemuroides* lies more distally. There is also a small secondary cusp between the hypoconid and hypoconulid of *P. leuroides* that is not present on the School Well specemen. The hypoconulid of School Well individual is rounded, bulbous and extends posteriorly while the cusp in *P. lemuroides* does not extend as far distally. The entoconid of the School Well individual leaves the talonid basin open lingually while that of *P. lemuroides* is closed. The difference in height of the cusps on the talonid and trigonid is much less exaggerated in *P. lemuroides* than in the School Well individual.

Promioclaenus pipiringosi

p4: There are strong similarities pertaining to the talonid of both samples. There are two cusps; one is slightly larger and lies bucally and a smaller one lies lingually. The difference amongst MOR 815d and P. pipiringosi samples lie in the trigonid. The paraconid that is found on MOR 815d individual is absent in P. pipiringosi. There is also a rudimentary metacone on the distal buccal side of MOR 815d that is also absent in *P. pipiringosi.*

m1: *P.pipiringosi's* m1 is narrower than its m2, which is not the case in the School Well individual. *P. pipiringosi* has the presence of a more pronounced hypoconulid extending distally. *P. pipiringosi* also has a more inflated entoconid compared with that the the School Well individual.

m2: The entoconid and hypoconid are placed and oriented very similarly in both samples. There is shelf that extends buccal from the entoconid MOR 815c that appears to be absent in P. pipiringosi.